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# EFFECTS OF EARLY STARVATION PERIODS ON ZOEAL DEVELOPMENT OF BRACHYURAN CRABS

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## Abstract

Larvae of the crabs *Menippe mercenaria* Say (Menippidae), *Panopeus herbstii* Milne-Edwards, *Neopanope sayi* Smith (Xanthidae), *Sesarma cinereum* Bosc (Grapsidae), and *Libinia emarginata* Leach (Majidae) were reared in the laboratory. Starvation periods different in length and timing within the first zoeal stage were studied as to their effects on later development and survival rate. After 1–3 days of initial feeding, most larvae had accumlated enough reserves to reach the second stage, independently of further food availability. The development of the survivors was delayed in the following stages, and their later mortality rate was higher than the fed controls. Starvation periods commencing directly after hatching of the larvae exert far stronger negative effects than those beginning later. All observations suggest a particularly sensitive phase in the beginning of larval life in brachyurans. When initial starvation periods exceed the point-of-no-return (PNR), the larvae will die later, even if feeding begins long before the energy reserves are depleted. Temporary lack of suitable prey may be an ecological factor controlling the survival of crab larvae as effectively as physical factors.

## Introduction

The larvae of a great number of brachyuran crab species have been reared under different environmental conditions in the laboratory, especially under varying temperatures and salinities. However, few studies consider the influence of varying food levels, and even fewer investigated the effects of temporary absence of suitable food on later development and survival. As pointed out by Anger and Dawirs (1981), such periods of starvation should be expected in a natural, variable environment. Thus, experimental data gained in cultures with extremely high food densities (this applies to most of the literature) indicate the potential survival and development rate under close-to-optimum conditions, rather than realistic figures to be expected in nature.

Anger and Dawirs (1981) found in larvae of the spider crab *Hyas araneus* that temporary lack of prey during the first zoeal stage could exert different effects on survival and development rates of both zoeal instars. The kind and extent of these effects was related to the timing and duration of the starvation periods. Several of their observations were in good agreement with those reported in the literature (Kurata, 1959; Yatsuzuka, 1962; Modin and Cox, 1967; Kon, 1979; Paul and Paul,

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Abbreviations: Z-1, Z-2, zoeal stages 1, 2, etc.; PNR, point of no return (*sensu* Blaxter and Hempel, 1963): length of starvation after which a re-fed larva cannot recover; PRS, point of reserve saturation (*sensu* Anger and Dawirs, 1981): point at which larvae have enough reserves to molt independent of further food supply.

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1980). This correspondence suggested the existence of some general response patterns common to many decapod larvae exposed to temporary early starvation.

The present study attempts to find such general trends in zoeal development of brachyurans and to distinguish them from species-specific responses.

## Materials and Methods

In summer 1980, ovigerous females of five brachyuran species were collected near Beaufort, North Carolina, and brought to the Duke University Marine Laboratory. The five were *Menippe mercenaria* Say (Menippidae), *Panopeus herbstii* Milne-Edwards, *Neopanope sayi* Smith (Xanthidae), *Sesarma cinereum* Bosc (Grapsidae), and *Libinia emarginata* Leach (Majidae).

*M. mercenaria* and *L. emarginata* were kept in large running seawater tables until their larvae were almost ready to hatch. Then they were transferred to smaller aerated aquaria (*ca.* 5 l capacity), from which the larvae were isolated a few hours after hatching. The other species, which are smaller, were maintained in bowls with *ca.* 1 l seawater. Water was changed daily, and the crabs were not fed until the larvae hatched and were isolated.

Taking into consideration the place of origin of the ovigerous females, as well as tests reported in the literature, the following salinities were applied in incubating and rearing the larvae: 30‰ in *M. mercenaria* (*cf.* Ong and Costlow, 1970), 25‰ in *P. herbstii, N. sayi,* and *S. cinereum* (*cf.* Costlow *et al.*, 1960, 1962), and 35‰ in *L. emarginata* (*cf.* Johns and Lang, 1977). Many larvae of *P. herbstii* and *N. sayi* died, presumably due to unsuitable salinity, but also possibly because the hatches were not sufficiently viable. The experiment with larvae of *P. herbstii* was repeated later at 35‰ with better success. Salinities were obtained by mixing filtered seawater (Gelman glassfiber filter type A/E) with sufficient amounts of deionized freshwater, and were checked by means of a refractometer. All experiments were carried out at 25°C in constant-temperature cabinets, with a 12:12 L:D photoperiod.

Larvae were transferred individually with large-bore pipettes into numbered vials containing *ca.* 15–20 ml seawater and (where applicable) *ca.* 100–200 freshly hatched *Artemia salina* nauplii (San Francisco Bay Strain lot #1737). Approximately every 23–25 h, water and food were changed and molts or mortality of individual larvae were recorded. Experiments were finished when all larvae had either died or metamorphosed to the megalopa stage. No attempts were made to rear megalopa further. Larvae were considered dead when they were opaque, or when no movement of any appendage or interanl structure could be seen under moderate magnification.

Each experiment (one species) comprised eight sets (subexperiments) of 25 larvae each. In each subexperiment a different feeding regimen was tested:

1. Food was provided only during the first *ca.* 24 h following hatching. The larvae were then transferred to clean vials after being washed in baths of filtered seawater to avoid accidental transfer of food organisms. No further feeding was done until a larva successfully molted to the second stage.
2. Same as (1), but initial feeding period 2 days.
3. Same as (1), but initial feeding period 3 days.
4. No starvation (fed control).
5. Starvation only during first ca. 24 h after hatching; then feeding.
6. Same as (5), but initial starvation period 2 days.

7. Same as (5), but initial starvation period 3 days.
8. No feeding period (starved control).

If not otherwise stated, mean values of time spans are given as arithmetic mean ± 95% confidence intervals (the latter only when $n > 3$). Differences between mean values were tested after comparing their variances ($F$ test) by means of Student's $t$ statistic. They were considered statistically significant if $p$ (two-tailed) was $<0.05$.

Mean durations of particular stages do not necessarily add to the cumulative figures (Tables I and II) unless there was no mortality.

The abbreviations Z-1, Z-2, etc. denote zoeal stages 1, 2, etc. Numbers of subexperiments (*e.g.* 4 = fed control) refer to the feeding regimens described above.

## Results

### *Rate of development and survival*

Figures 1 and 2 give development and mortality rates for the first two zoeal stages of two representative species (*Menippe mercenaria* and *Panopeus herbstii*). The starved control group (8) is omitted, because no larvae reached the second stage.

Under condition 1 (1 day of initial feeding) only a few larvae of *Libinia emarginata* and *Neopanope sayi* reached the Z-2 stage. None survived to metamorphosis (megalopa).

Mortality figures for the Z-2 are given in Figures 1 and 2 as percentage of larvae which survived to this instar. Further data are presented in Tables I and II.

### *Menippe mercenaria*

In the fed controls (4, Table I), 68% of the larvae reached megalopa stage after 17.85 ± 0.60 days. Starvation always delayed development and increased mortality as compared to this control group. Larvae initially fed for 2–3 days before starvation began had lowered survival in the Z-1 stage, but also slightly (statistically insignificant) shortened development to the second zoea. The Z-2, however, which was not starved itself, showed a significant prolongation (Fig. 1). Duration of Z-3 also increased (Table I).

When lack of prey occurred directly after hatching (subexperiments 5–7; Table I, Fig. 1), another pattern was observed: The Z-1 stage was significantly prolonged. After only 1 day of initial starvation, this delay was a little shorter than 1 day, but it was 3.55 days after 2 days starvation. In the latter subexperiment (subexperiment 6) mortality also strongly increased in the first two stages. After 3 days without food (subexperiment 7), no larva recovered after re-feeding.

Initial starvation in the Z-1 apparently caused a weak shortening of the duration of the following instar (Fig. 1). In the Z-3 and Z-4 some delay was noted (Table I), but it was statistically not significant.

### *Panopeus herbstii*

The first experiment with *P. herbstii*, carried out at a salinity of 25‰, resulted in low survival, delayed development, and high variation in molt frequency. It remains in question whether this was due to unsuitably low salinity or low genetic viability of the hatch. The results are included in Table I because they still show a pattern:

In the fed control group (subexperiment 4) 64% of the larvae reached the second instar after 5.56 ± 0.76 days. Z-1 duration was shortened in subexperiments 2 and

TABLE I

M. mercenaria *and* P. herbstii: *Duration of zoeal stages and of cumulative development (cum.) in days (mean ± 95% confidence intervals), and mortality (%) given different feeding regimens (see text for details of regimens).*

| | | Feeding regimen | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | | | 3 | | | 4 | | | 5 | | | 6 | | | 7 | | |
| | | | days | | | days | | | days | | | days | | | days | | | days | | |
| Species | Stage | % | x̄ | ± | % | x̄ | ± | % | x̄ | ± | % | x̄ | ± | % | x̄ | ± | % | x̄ | ± | % |
| *Menippe mercenaria* | Z-1 | 100 | 3.50 | 0.75 | 72 | 3.50 | 0.37 | 20 | 4.09 | 0.54 | 12 | 4.91 | 0.79 | 32 | 7.64 | 0.99 | 72 | | | 100 |
| | Z-2 | | 4.67 | 0.54 | 4 | 3.92 | 0.33 | 8 | 3.42 | 0.24 | 12 | 3.07 | 0.39 | 8 | 3.00 | 0 | 12 | | | |
| | cum. | | 8.00 | 1.22 | 76 | 7.75 | 0.55 | 28 | 7.24 | 0.25 | 24 | 7.70 | 0.48 | 40 | 10.25 | 0.80 | 84 | | | |
| | Z-3 | | 2.67 | 0.68 | 0 | 2.90 | 0.57 | 4 | 2.56 | 0.25 | 4 | 2.71 | 0.42 | 4 | 4.67 | | 4 | | | |
| | cum. | | 10.67 | 1.23 | 76 | 10.67 | 0.76 | 32 | 9.83 | 0.42 | 28 | 10.43 | 0.48 | 44 | 14.83 | | 88 | | | |
| | Z-4 | | 3.33 | 0.54 | 0 | 3.75 | 0.82 | 0 | 3.29 | 0.24 | 4 | 3.71 | 0.56 | 0 | 3.67 | | 0 | | | |
| | cum. | | 14.00 | 1.10 | 76 | 14.42 | 1.42 | 32 | 13.21 | 0.51 | 32 | 14.14 | 0.86 | 44 | 18.50 | | 88 | | | |
| | Z-5 | | 5.60 | 2.42 | 4 | 4.40 | 0.50 | 12 | 4.67 | 0.36 | 0 | 4.77 | 0.56 | 4 | 4.50 | | 4 | | | |
| | cum. | | 19.30 | 3.21 | 80 | 18.90 | 1.48 | 44 | 17.85 | 0.60 | 32 | 18.73 | 1.02 | 48 | 21.00 | | 92 | | | |
| *Panopeus herbstii* 25‰ | Z-1 | 100 | 3.50 | | 96 | 3.50 | 0 | 84 | 5.56 | 0.76 | 36 | 6.33 | 1.11 | 52 | | | 100 | | | 100 |
| | Z-2 | | | | 4 | 5.00 | | 8 | 4.00 | | 56 | 3.33 | | 36 | | | | | | |
| | cum. | | | | 100 | 8.50 | | 92 | 7.50 | | 92 | 8.50 | | 88 | | | | | | |
| *Panopeus herbstii* 35‰ | Z-1 | 100 | 2.55 | 0.10 | 16 | 2.78 | 0.19 | 0 | 2.54 | 0.08 | 0 | 3.66 | 0.15 | 0 | 5.35 | 0.17 | 16 | 7.17 | | 88 |
| | Z-2 | | 3.14 | 0.22 | 0 | 2.88 | 0.23 | 4 | 2.52 | 0.21 | 0 | 2.86 | 0.15 | 8 | 3.00 | 0.36 | 0 | 3.00 | | 4 |
| | cum. | | 5.69 | 0.27 | 16 | 5.67 | 0.30 | 4 | 5.06 | 0.21 | 0 | 6.54 | 0.16 | 8 | 8.35 | 0.27 | 16 | 10.00 | | 92 |
| | Z-3 | | 3.05 | 0.18 | 4 | 2.96 | 0.36 | 4 | 2.79 | 0.25 | 4 | 3.11 | 0.29 | 20 | 3.00 | 0.36 | 16 | 3.00 | | 0 |
| | cum. | | 8.75 | 0.34 | 20 | 8.59 | 0.49 | 8 | 7.88 | 0.21 | 4 | 9.67 | 0.39 | 28 | 11.38 | 0.36 | 32 | 13.00 | | 92 |
| | Z-4 | | 3.76 | 0.22 | 12 | 4.31 | 0.26 | 28 | 4.07 | 0.57 | 36 | 3.57 | 0.30 | 16 | 3.82 | 0.40 | 24 | 4.00 | | 4 |
| | cum. | | 12.56 | 0.34 | 32 | 12.75 | 0.53 | 36 | 11.90 | 0.69 | 40 | 13.29 | 0.52 | 44 | 15.14 | 0.34 | 56 | 17.50 | | 96 |

TABLE II

N. sayi, S. cinereum, *and* L. emarginata*: Duration of zoeal stages and of cumulative development (cum.) in days (mean ± 95% confidence intervals), and mortality (%) given different feeding regimens (see text for details of regimens).*

| | | Feeding regimen | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | | | 2 | | | 3 | | | 4 | | | 5 | | | 6 | | | 7 | | |
| | | days | | | days | | | days | | | days | | | days | | | days | | | days | | |
| Species | Stage | x̄ | ± | % | x̄ | ± | % | x̄ | ± | % | x̄ | ± | % | x̄ | ± | % | x̄ | ± | % | x̄ | ± | % |
| *Neopanope sayi* | Z-1 | 4.50 | | 96 | 3.28 | 0.34 | 64 | 3.41 | 0.36 | 56 | 4.13 | 0.42 | 16 | 5.88 | 0.62 | 68 | | | 100 | | | 100 |
| | Z-2 | | | 4 | | | 36 | 5.00 | 0.88 | 24 | 4.41 | 0.37 | 16 | 4.00 | | 20 | | | | | | |
| | cum. | | | 100 | | | 100 | 8.50 | 0.88 | 80 | 8.21 | 0.57 | 32 | 9.50 | | 88 | | | | | | |
| | Z-3 | | | | | | | 5.67 | 1.43 | 8 | 5.10 | 0.63 | 28 | 4.50 | | 4 | | | | | | |
| | cum. | | | | | | | 14.50 | | 88 | 13.10 | 1.40 | 60 | 14.00 | | 92 | | | | | | |
| *Sesarma cinereum* | Z-1 | | | 100 | 3.25 | 0.29 | 52 | 3.17 | 0.26 | 16 | 3.24 | 0.35 | 8 | 4.11 | 0.42 | 28 | 6.17 | 1.27 | 6 | 9.50 | | 96 |
| | Z-2 | | | | 5.17 | 0.43 | 12 | 3.20 | 0.45 | 8 | 2.69 | 0.26 | 12 | 4.07 | 0.80 | 12 | 4.50 | 3.04 | 8 | 2.00 | | 0 |
| | cum. | | | | 8.67 | 0.43 | 64 | 6.70 | 0.45 | 24 | 5.94 | 0.22 | 20 | 8.03 | 0.83 | 40 | 10.25 | 2.72 | 84 | 11.50 | | 96 |
| | Z-3 | | | | 3.16 | 0.54 | 0 | 3.20 | 0.45 | 0 | 2.94 | 0.31 | 8 | 3.73 | 0.99 | 0 | 4.50 | 2.05 | 0 | 5.00 | | 0 |
| | cum. | | | | 11.83 | 1.08 | 64 | 9.90 | 0.60 | 24 | 8.88 | 0.47 | 28 | 11.77 | 1.57 | 40 | 14.75 | 4.57 | 84 | 16.50 | | 96 |
| | Z-4 | | | | 4.33 | 0.68 | 12 | 4.36 | 0.45 | 4 | 3.88 | 0.38 | 4 | 3.86 | 0.45 | 16 | 5.75 | 1.52 | 0 | 6.00 | | 0 |
| | cum. | | | | 15.50 | 2.39 | 76 | 14.20 | 0.68 | 28 | 12.70 | 0.93 | 32 | 14.86 | 1.09 | 56 | 20.50 | 4.31 | 84 | 22.50 | | 96 |
| *Libinia emarginata* | Z-1 | 3.43 | 0.27 | 44 | 2.92 | 0.24 | 24 | 2.60 | 0.14 | 16 | 2.62 | 0.18 | 36 | 3.67 | 0.25 | 52 | 6.04 | 0.46 | 56 | 6.50 | | 96 |
| | Z-2 | | | 56 | 4.14 | 0.35 | 48 | 3.40 | 0.28 | 24 | 3.27 | 0.31 | 20 | 4.00 | | 40 | 4.50 | 0.57 | 20 | | | 4 |
| | cum. | | | 100 | 6.79 | 0.45 | 72 | 5.97 | 0.29 | 40 | 5.95 | 0.31 | 56 | 7.50 | | 92 | 10.50 | 0.66 | 76 | | | 100 |

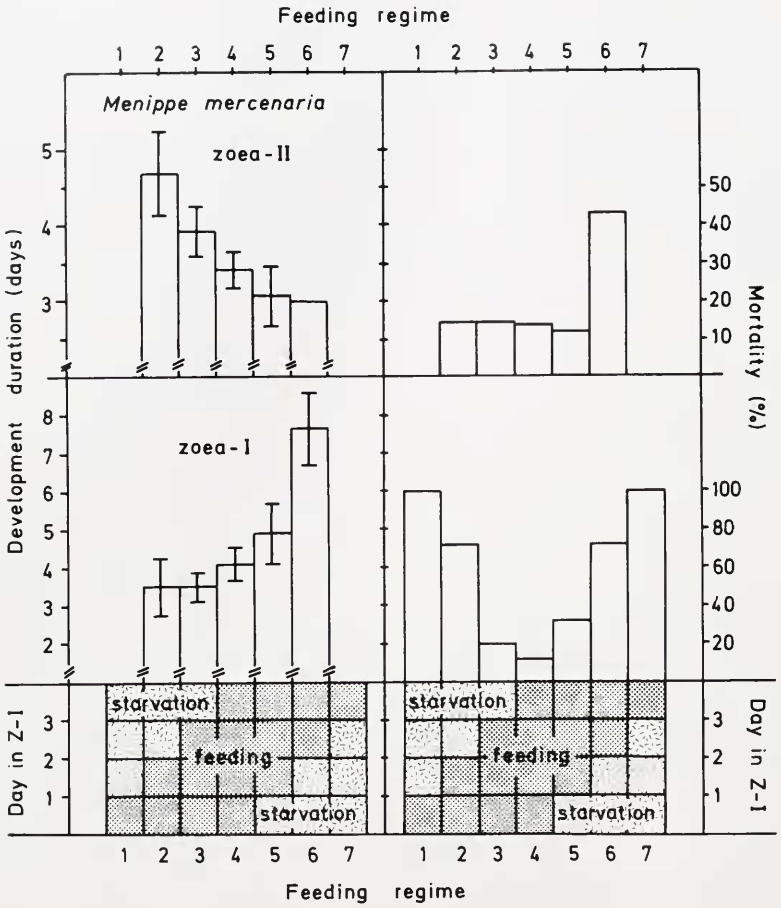


FIGURE 1. *Menippe mercenaria*: Development duration (days; mean ± 95% confidence intervals) and mortality (%) in the first and second larval instars in relation to the feeding regime (feeding/starvation schedule) during the zoea-1 stage.

3. Due to low survival, delay in Z-2 duration (as observed in *M. mercenaria* in these subexperiments) was only visible in feeding regimen 3: Z-2 lasted 1 day longer than in the fed control.

Initial starvation of 2–3 days (subexperiments 6 and 7) caused 100% mortality in the Z-1 stage. As in *M. mercenaria*, one day of starvation at the beginning of the first zoeal instar lowered survival and delayed Z-1 less than 1 day.

The second experiment with *P. herbstii* (35‰ salinity) yielded far better results: In the fed control group there was no mortality until stage 3. Only in the Z-4 instar did many larvae die when attempting to molt to the megalopa.

Starvation at the end of the Z-1 stage did not influence its duration (Table I; Fig. 2), but as in the last two experiments, it significantly lengthened the Z-2 stage. As in *M. mercenaria*, the Z-3 also was slightly (statistically insignificantly) lengthened.

Starvation beginning directly after hatching again caused a considerable, statistically significant lengthening of Z-1 duration (Fig. 2). However, unlike the case

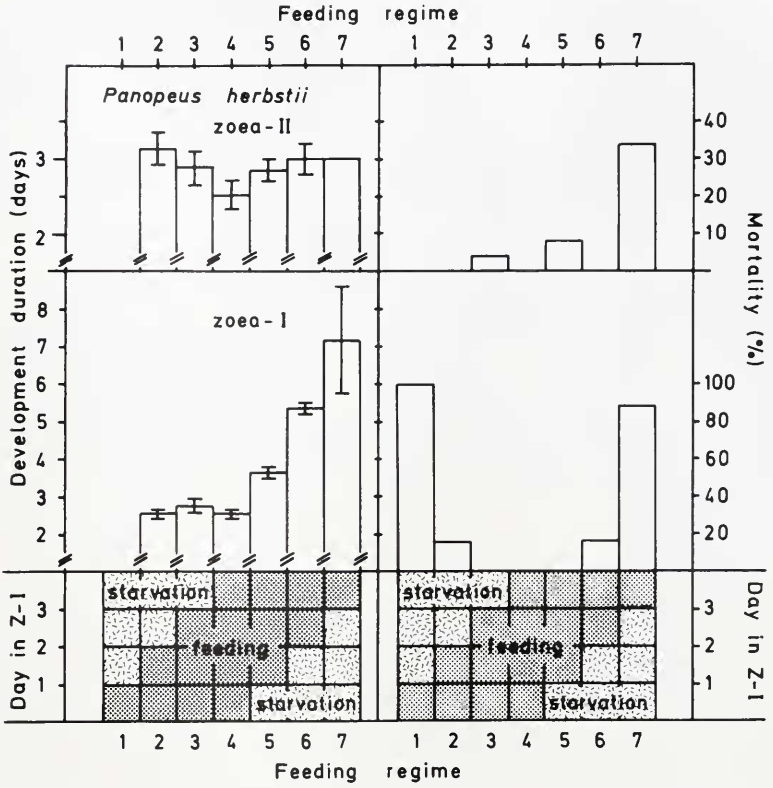


FIGURE 2. *Panopeus herbstii*: Development duration (days; mean ± 95% confidence intervals) and mortality (%) in the first and second larval instar in relation to the feeding regime (feeding/starvation schedule) during the zoea-1 stage.

in the previously described species, Z-2 was also significantly lengthened. Z-3 duration also was slightly prolonged. Since these effects are additive, even short initial lack of food caused a statistically significant delay in development to the megalopa. Mortality also was higher following initial starvation periods (Table I).

*Neopanope sayi*

As in the first experiment with *P. herbstii*, some factor caused high mortality in this species; none reached the megalopa stage (Table II).

Starvation during the first zoeal stage again increased mortality. Starvation at the end of this instar, did not clearly affect its duration, whereas the Z-2 was lengthened somewhat (Table II).

After 2–3 days of initial starvation, all larvae died in the Z-1. If this lack of food lasted for only 1 day, 32% of the larvae successfully molted to the Z-2 stage, with a delay of 1.75 days compared to fed controls. The few survivors reaching the next instar had a slightly shortened Z-2 development (4 days in contrast to 4.41 ± 0.37 in the control).

*Sesarma cinereum*

In fed controls (subexperiment 4) 68% of the larvae molted to the megalopa, 12.70 ± 0.93 days after hatching.

Survival and total development time were considerably affected by early starvation periods (Table II):

Duration of the Z-1 stage was not influenced by lack of food occurring at its end (Table II), but survival to the second zoea was lowered, and the Z-2 and Z-3 stages were prolonged.

In subexperiment 2, two different groups of larvae were considered separately:

1. Those that molted to Z-2 one day after commencement of starvation later did not show significantly delayed development nor any mortality in the Z-2 stage. Also, the Z-3 stage showed no difference from the fed controls.

2. Larvae that molted 2 days after commencement of starvation had a significantly prolonged Z-2, and their mortality increased. The Z-3 stage also was significantly prolonged (5.17 ± 0.43 vs. 2.94 ± 0.31 days in the fed control group).

In subexperiments in which the *S. cinereum* larvae were starved initially (5–7), the Z-1 stage was significantly prolonged and mortality increased (Table II), as in the species discussed previously. The duration of the Z-2 did not clearly change. However, all later zoeal stages became longer in relation to longer starvation periods. As in all species previously discussed, starvation periods had a far stronger effect when they occurred right after hatching, rather than later.

### *Libinia emarginata*

The mortality pattern in larvae of the spider crab *L. emarginata* was veiled by high death rates in the beginning of the experiment. Development duration, was as in most cases, more strongly correlated to early starvation (Table II). Both zoeal stages were significantly prolonged due to lack of food, regardless of the timing of starvation. This effect, however, was again much more conspicuous when starvation took place in the beginning of the Z-1.

As in *S. cinereum*, the survivors of subexperiment 2 were considered in two groups according to their time of molting to the Z-2 stage: Only one out of eight larvae that had molted to the Z-2 during the fourth day after hatching (*i.e.*, after 2 days starvation) later successfully molted to the megalopa. In the other group, which had reached the Z-2 during the third day, six out of eleven larvae later became megalopae.

### *Mortality patterns*

Four types of mortality may be distinguished:

1. Initial mortality: During the first 2 days of experiments, death rates were often relatively high regardless of feeding regimens. This type of mortality, strongest in *L. emarginata*, is rather unpredictable. It is related to low viability of individual larvae unable to adjust to the experimental conditions.

2. Mortality before and during molting: Larvae normally have higher death rates during molting periods than during intermolt. Short starvation periods at the beginning of the Z-1 stage (subexperiments 5 and 6), often increased this type of mortality drastically. It was most conspicuous in *P. herbstii, S. cinereum,* and *L. emarginata.*

3. Mortality after re-feeding: Larvae initially starved for 2–3 days often had high death rates during the first 2 days following feeding. This effect was obvious in all species except *S. cinereum*; it was strongest after 3 days of initial lack of prey (subexperiment 7). *M. mercenaria, P. herbstii* (first experiment), and *L. emarginata* larvae treated this way had significantly shorter mean survival times

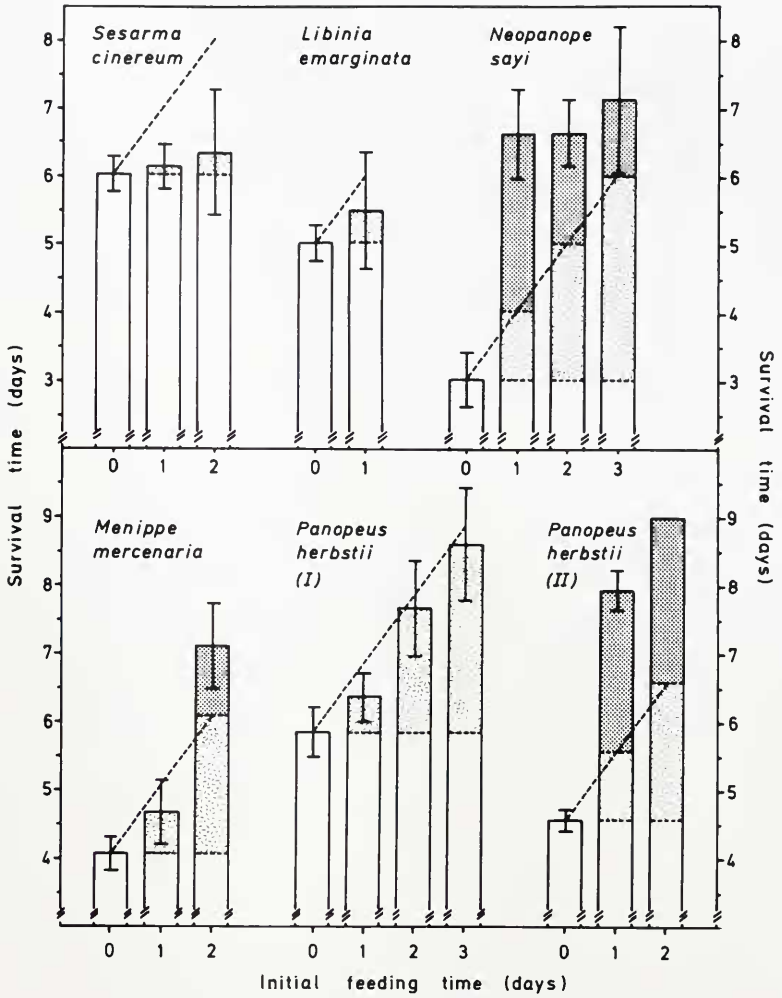


FIGURE 3. Survival time (days; mean ± 95% confidence intervals) in crab larvae (first stage) starved after different feeding periods. Dotted lines: Survival time in the starved control (0 days) plus duration of feeding period. For further explanation see text.

than those in the completely starved control (subexperiment 8). The figures were 3.42 ± 0.35 versus 4.08 ± 0.25 days in the first species, 5.04 ± 0.35 versus 5.86 ± 0.36 days in the second, and 4.27 ± 0.36 versus 5.02 ± 0.26 days in the third.

4. Death due to depletion of reserves: In the starved control group, larvae died mostly in well-defined periods of time. These periods of time could be used to show the detrimental effect of too late re-feeding (see above) or to test the larvae's food uptake afte starvation: In *N. sayi*, for example, it did not make any difference whether the larvae were re-fed after 2 or 3 days or never. The survival times were not significantly different, *i.e.*, the larvae must have lost their ability to catch or to eat prey. The same effect was observed in *S. cinereum* in subexperiment 7.

The starved control group made possible comparison (Fig. 3) of the mean survival time in those larvae which were fed for some time before starvation (sub-

experiments 1–3), but did not reach the Z-2 stage, with the sum of the survival time under complete starvation (subexperiment 8) plus the initial feeding period (represented by dotted lines in Fig. 3). Three effects were observed:

1. Survival was prolonged approximately by the time span of initial feeding, *i.e.*, during each day of feeding enough reserves were accumulated to survive 1 later day of starvation (slightly shaded parts of bars in Fig. 3). This type of response was found in *P. herbstii* (first experiment) and in subexperiment 1 in *M. mercenaria* and *L. emarginata*.

2. Survival was prolonged by more than the feeding period (dark shaded part of bars in Fig. 3), indicating a comparatively fast rate of reserve accumulation. This pattern was observed in *P. herbstii* (second experiment), *N. sayi*, and in part in *M. mercenaria*.

3. Initial feeding periods did not significantly influence survival time under later starvation. Only in *S. cinereum* was such weak accumulation of reserves found.

## Discussion

If a marine environment is variable, and characterized by temporary lack of suitable prey (patchiness in time and space) then our observations have an important ecological implication: Even short starvation periods in early larval development of brachyurans can severely affect their later chance of survival. These negative effects, such as increased mortality and delayed development, might be at least as significant as those exerted by variations in temperature and salinity.

The present study concerned whether general effects were common to brachyuran larvae subjected to temporary starvation. Some lethal and sublethal effects are summarized in Figure 4. To average all observed effects exerted on development duration, a "development factor" was calculated for every feeding regimen. This index sets the stage durations in the fed control (subexperiment 4) at 1.0. If, for example, a given stage in a subexperiment is prolonged to double the control figure, the development factor is 2.0; if it was shortened to 80% of the control value, then the index is 0.8. Mean values and standard deviations were obtained in this way from all experiments (Fig. 4). Figures represented by single individuals only were omitted from this presentation. The mortality values in the graph were arc-sin transformed before averaging.

Short starvation at the end of the Z-1 did not strongly affect the duration of this instar. In *L. emarginata* it significantly prolonged the stage, but in the other species it had no effect or shortened the stage. The longer this starvation (*i.e.*, the shorter the initial feeding period) the higher was mortality in Z-1. In some species (*cf.* Table II), the stage tended to be longer when starvation commenced after only 1 day of feeding. Anger and Dawirs (1981) found a similar pattern in *Hyas araneus*: Short periods without food at the end of the Z-1 stage appeared to slightly shorten this stage, whereas long periods lengthened it. This effect is too weak and may depend too much on the species (see *L. emarginata*) for speculation on its causes without further observations.

The experimental design for subexperiments 1–4 was too rough to determine exact values for the point-of-reserve-saturation ($PRS_0$; Anger & Dawirs, 1981). In most species considered here it was more than 1, but less than 2 days. Only in *L. emarginata* was even the $PRS_{50}$ below 1 day, *i.e.* 50% of the larvae had accumulated enough reserves at this time to molt successfully to the Z-2 stage without

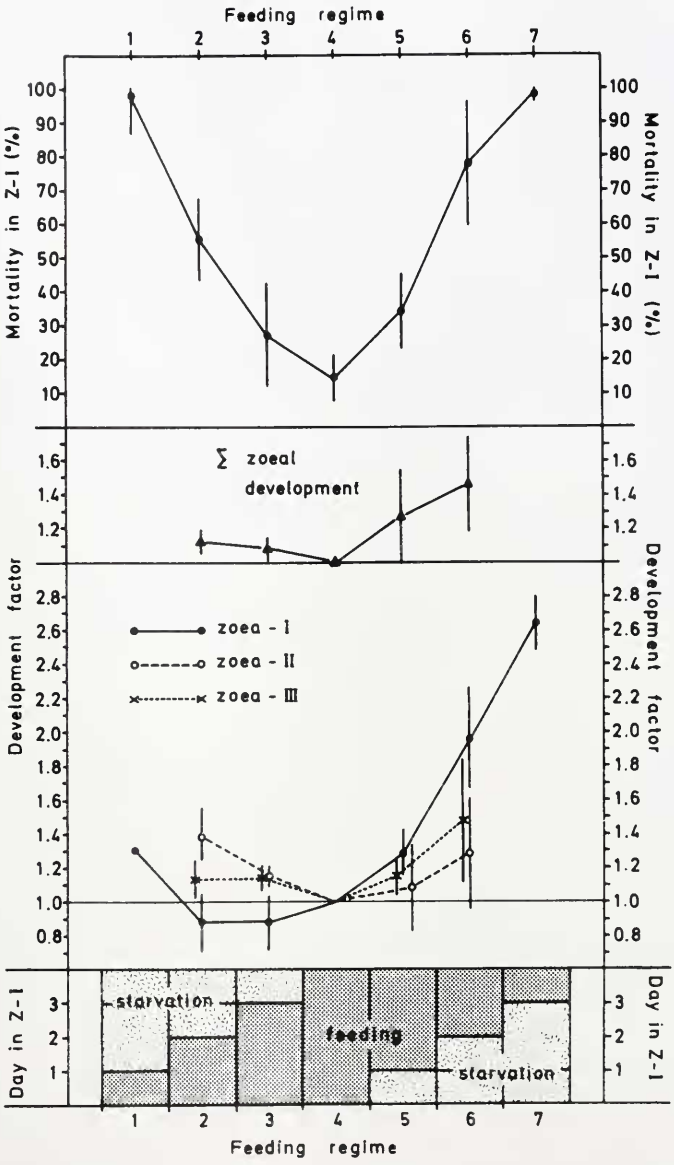


FIGURE 4. Change in development duration, expressed as multiple of fed control (= feeding regimen no. 4), and mortality (%) in zoeal development of crab larvae in relation to feeding/starvation schedule during the first stage: Averaged effects from all experiments (mean ± standard deviation).

further food supply (Table II). The mean $PRS_{50}$ value of all species was *ca.* 2 days (Fig. 4).

The amount of reserves accumulated during early feeding periods probably is not only species-dependent, but is also influenced by other factors (Fig. 3): In the first experiment with *P. herbstii*, during each day of feeding a reserve for about

1 day of future starvation was accumulated. In the second experiment, much more reserves were stored.

Individual variability also plays a role: As shown in subexperiment 2 in *S. cinereum* and *L. emarginata*, larvae that molted sooner than others to the Z-2 stage were much less affected by starvation before the molt. Though the same age, they apparently had developed faster and consequently were further advanced when starvation commenced, giving them a better chance of survival than slower-growing siblings.

In all experiments in this study, starvation commencing toward the end of the Z-1 stage significantly prolonged the Z-2, and to a lesser degree the following stage (Fig. 4). The same effect was found by Anger and Dawirs (1981) in *H. araneus* larvae. In the present study, death rates during the Z-2 instar also increased in most cases where the Z-1 had been starved before molting (Table II). Since the lengthening in later stages was longer than the shortening of Z-1, starvation toward the end of Z-1 caused, on an average, a weak prolongation in total zoeal development (Fig. 4).

Any starvation period at the beginning of the Z-1 caused a highly significant lengthening of this stage in all species considered (Figs. 1 and 2; 4). The same was observed in other brachyuran species by Kon (1979), Anger and Dawirs (1981), and by Dawirs (unpublished). This effect is apparently a general response pattern: Zoeal development apparently does not begin to use existing reserves from the egg, unless some essential cue is provided by food taken up. Anger and Dawirs (1981) discussed possible mechanisms in early larval reconstruction processes and suggested that sterols, precursors of the molting hormone ecdysterone, may play a crucial role as a starting cue. As in the present study, they found that the delay was approximately equivalent to the duration of the starvation period in Z-1 larvae of *H. araneus*. This indicates that except for chitin synthesis (see Anger and Nair, 1979) developmental processes awaited the starting signal given by first feeding. When the time span without food supply increased, the delay corresponding to this period was further increased, during which time lost reserves may have had to be replenished.

In all experiments of this type, a "point-of-no-return" (PNR; for recent discussion see Anger and Dawirs, 1981) was observed, mostly long before the energy reserves were ultimately depleted. The time when 50% of the starved larvae could not recover when being re-fed ($PNR_{50}$) was short in the species investigated here: Mostly it was *ca.* 1–2 days, *i.e.* considerably shorter than the survival time under continuous starvation (cf. Fig. 3). The high difference between the PNR levels in the two experiments with *P. herbstii* (Table I) that showed this measure of starvation resistance probably is also influenced by other factors, such as perhaps salinity. Early starvation periods lasting 1–3 days strongly increased deaths in the first zoeal stage (Fig. 4). Later survival also tended to decrease (Figs. 1 and 2). The influence of such starvation immediately following hatching was apparently always stronger than where a feeding period preceded starvation (subexperiments 1–3).

The effects of initial lack of prey on Z-2 duration were not uniform: In *P. herbstii, S. cinereum,* and *L. emarginata* a lengthening was found, but in the other two species a slight shortening. The latter effect was also observed by Anger and Dawirs (1981) in *H. araneus* larvae. Surprisingly, in all species of the present study there was some prolongation of the Z-3 stage, and in some instances even of the Z-4 (Tables I and II). The effect in the Z-3 was on an average even stronger than

the delay in the Z-2 (Fig. 4). As a consequence of these patterns, the whole zoeal development to the megalopa was clearly delayed. These effects of initial starvation were much stronger than those caused by later fasting (Fig. 4): When suitable prey was absent during only the first 48 h of larval life, zoeal development was delayed at an average by almost 50%, and almost 80% of the larvae did not even reach the second instar.

Our results confirm a particularly critical period in the beginning of larval development of brachyuran crabs (Kon, 1979; Anger and Dawirs, 1981) and perhaps also in other decapods (Kurata, 1959; Modin and Cox, 1967; Paul and Paul, 1980). The latter authors observed that early starvation in king crab zoeae lowered ability to catch prey after re-feeding. This effect was probably responsible for the similar survival times of re-fed and continuously starved larvae of some species in the present study. However, when initial fasting was short, survival usually was significantly prolonged in larvae not reaching the second stage (as compared to the starved control). This indicates that the larvae were still able to catch, ingest, and convert food, but had lost their ability to molt successfully. Anger and Dawirs (1981), who observed the same effect in spider crab larvae (*H. araneus*), suggested an irreversible damage to some hormonal or enzymatic system controlling molt. Biochemical studies combined with experiments as designed for the present investigation should explain the mechanisms involved. Future studies will also have to extend to later larval stages (especially to the megalopa) and to interactions of starvation with other ecological and biological factors.

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